11. *The Breeding and Growth of* Hymenosoma orbiculare Desm. (*Crustacea, Brachyura*). By G. J. Broekhuysen, Ph.D., Department of Zoology, University of Cape Town. (With 13 text figures.)

Introduction

The growth and reproduction of the South African shore crab *Cyclograpsus punctatus* was described earlier (Broekhuysen, 1941). The present paper deals with the Crown crab *Hymenosoma orbiculare*. Whereas *Cyclograpsus* lives on the upper part of the shore and is common among broken rocks, *Hymenosoma* lives on the lower part of the shore and is restricted to quiet areas where fine sands and mud accumulate. It is thus common in lagoons and estuaries. *Cyclograpsus* can withstand exposure to air for considerable periods and prefers this, but *Hymenosoma* either buries itself in damp sand covered by a shallow layer of

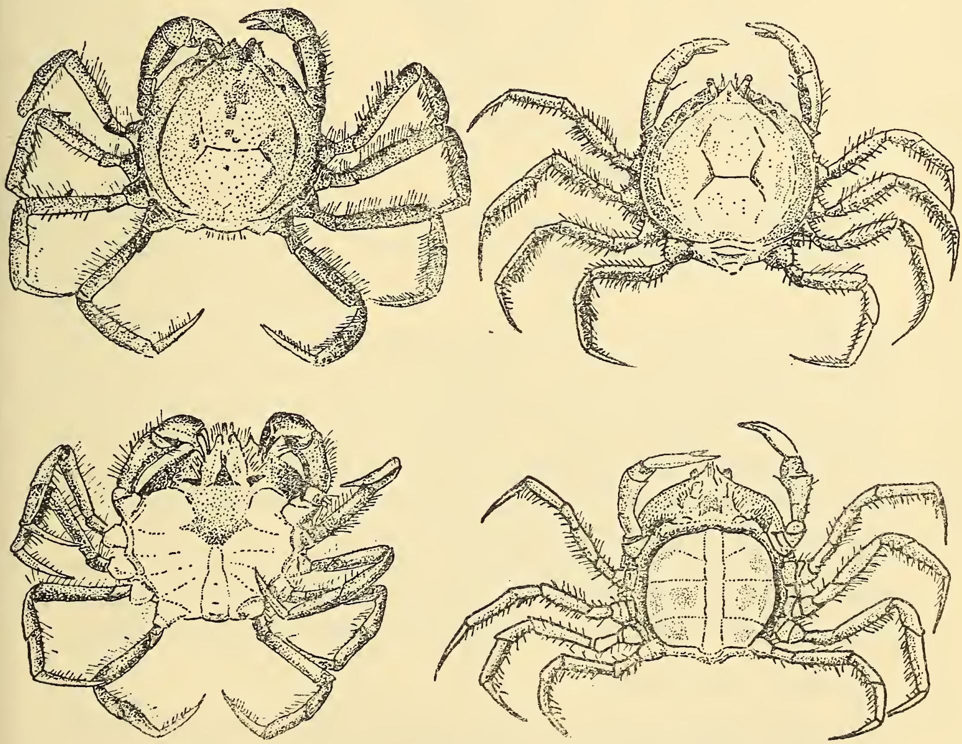

Fig. 1. *Hymenosoma orbiculare* Desm.
Large specimens from the Sand Vlei Estuary, natural size. Left: male; right: female.

water or moves down the shore with the ebbing tide and often extends below tide marks. Thus Barnard (1950) has recorded it from 45 fathoms. Nevertheless there are certain similarities between the two crabs: both tolerate a very wide range of temperature and salinity.

The ecological niche occupied by *H. orbiculare* shows much similarity to that occupied by *Carcinus maenas* of the Northern hemisphere (Broekhuysen, 1936). *Carcinus*, however, seems to prefer a more solid bottom than *Hymenosoma*, although the species was very common in the Wadden Sea, N.W. of Holland, where the bottom is sandy.

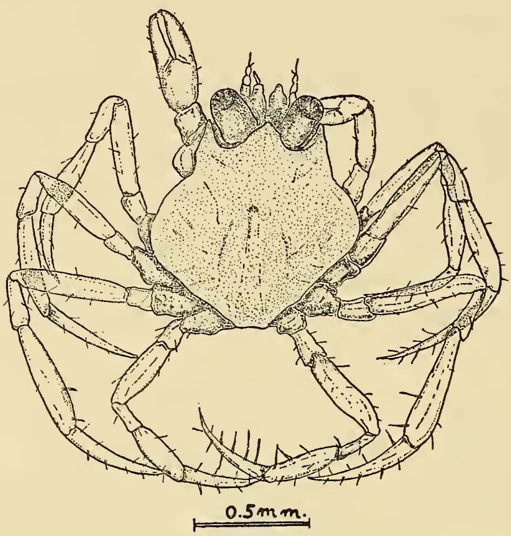

Fig. 2. *Hymenosoma orbiculare* Desm. First crab (post-larval) stage. A Megalopa stage has not been observed.

Hymenosoma orbiculare Desm. has been described by Barnard (1950). The adult ♂ and ♀ are illustrated in fig. 1; and in fig. 2 an example of the first crab (post-larval) stage. During the course of the estuary survey carried out by the University of Cape Town, the species has been recorded from the following localities: Lambert's Bay, Steenberg's Cove, Berg River Mouth, Saldanha Bay, Langebaan Lagoon, Milnerton Estuary, Hout Bay, Sand Vlei Estuary, False Bay, Klein River Lagoon, Breede River, Great Brak River Mouth, Knysna Lagoon, Sundays River Mouth, Bushman River Mouth, Keiskamma River Mouth, The Haven, Port St. Johns, Durban Bay, St. Lucia Bay, Kosi Bay, estuaries near Inhambane (Portuguese East Africa). Balss recorded it from Lüderitzbucht and Barnard from Olifants River Mouth, so that its total distribution is from South West Africa around the Cape to Portuguese East Africa (see fig. 3). Also recorded from Zanzibar (Lenz, 1905).

Hymenosoma geometricum Stimpson was described from False Bay. Barnard (1950) considers this to be merely a deep-water variety of *H. orbiculare*. The identity of the two species will be discussed further in the present paper.

Material and Methods

The bulk of the material was collected in Sand Vlei Estuary at Muizenberg between the Vlei Bridge and the Foot Bridge (see fig. 4). During the course of the investigation the estuary was subjected to wide variations in salinity

Fig. 3

A map of Southern Africa showing some of the stations from where *H. orbiculare* has been collected. (From Day, J. H., 'The Polychaet Fauna of South Africa.' *Ann. Natal Mus.*, XII, 3, 1953.)

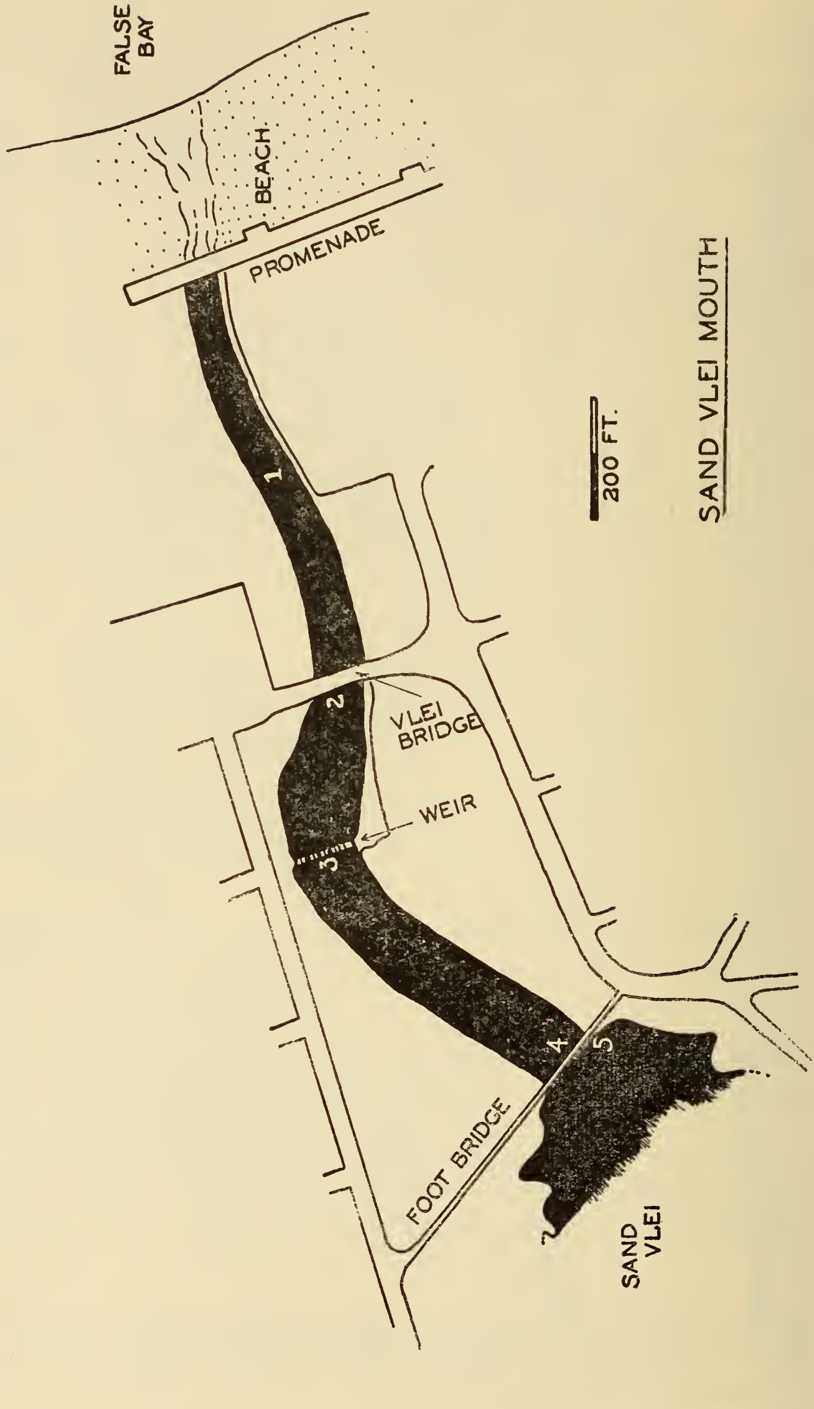

Fig. 4
The Mouth of Sand Vlei opening into False Bay.

indicated by a limited number of salinity determinations which have been tabulated in Table I.

Table I

Salinities determined in the Sand Vlei Estuary during the course of the investigation (see for stations fig. 4). The figures with an asterisk were bottom sample readings.

Station	*March*	*April*	*May*	*June*	*July*	*August*	*September*	*December*	*January*
1	—	8·31–9·0	7·4–7·6	3·3–31·8	0·5–5·8	—	33·7–34·3	—	—
2	7·7	8·4	7·2–7·5	2·8–25·0	0·4–5·7	0·5–0·6*	8·4–32·3	24·2	20·1
3	8·9	7·9	7·2–7·5	0·8–25·2	0·4–5·8	0·6	6·0–31·2		21·4
4		9·2	3·3–8·2 4·8*	2·0–23·1			1·5–28·9		21·5
5			2·8	3·3					

The salinites given in the above table are in $^{0}/_{00}$.

Random samples of crabs were collected at regular intervals from February 1947 to February 1948. The total was 1,494 females and 867 males. After sexing, the maximum width of the carapace was measured. The degree of maturity was judged from the shape of the abdomen, and the adults were dissected to determine the developmental stage of the gonads. Berried females were recorded and the developmental stage of the developing embryos noted.

During the course of the investigation a considerable number of *Hymenosoma* were kept in the laboratory. They were in glass dishes with a little water. Sand and shell fragments were provided as a substratum. These crabs were under constant observation.

The Reproductive Stages of the Male

A total of 752 males collected from Sand Vlei had a carapace breadth exceeding 14 mm. By dissecting, three stages could be distinguished in the reproductive system: (*a*) gonads undeveloped or small; (*b*) gonads developing; (*c*) gonads fully developed.

The monthly changes in the percentage of crabs which fell into these three categories is shown in Table II and text-figure 5.

Table II

Developmental Stages of the Gonads of Males from Sand Vlei during the period February 1947 to February 1948 (figures given are percentages).

Date	*Gonads undeveloped*	*Gonads developing*	*Gonads well developed*	*Total number of crabs*
February	1	38	61	94
March	5	26	69	175
April	4	13	83	78
May	10	24	65	78
June	4	26	70	23
July	0	28	72	25
August	2	37	61	41
September	–	–	–	1
October	–	–	–	3
November	67	2	31	52
December	21	54	26	39
January	8	41	51	143

No records are available for September and October as the water-level in the estuary was so high that collecting was difficult. It will be seen that most of the males had fully developed gonads between February and August. In November (and possibly October) they had small or resting gonads and in December to January they were growing.

It therefore appears that during spring and early summer most males were unable to copulate as their gonads were not mature. The breeding-season was in late summer and in winter, and covered a period of eight months. It must be stressed that these conclusions refer only to crabs in Sand Vlei Estuary and differences may well occur in crabs inhabiting other localities. Thus of 25 mature males caught at Lambert's Bay in October 1947, 4 per cent had undeveloped gonads, 12 per cent developing gonads, and 84 per cent well-developed gonads. As will be seen later, the developmental cycle of the male fits in rather well with that of the female.

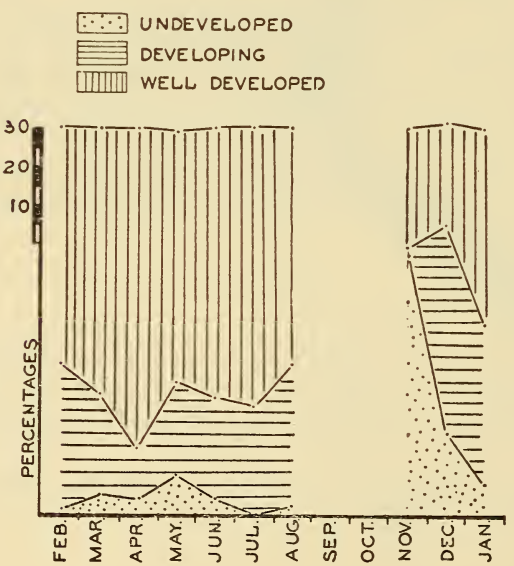

Fig. 5

The development of the gonads in males. During the months September and October too few males were obtained to make observations possible.

The Reproductive Stages of the Female

A total of 1,314 females with a carapace width exceeding 14 mm., were examined and of those which were not in berry, 687 were dissected and the state of the gonads recorded in the same three categories as was used for the males, namely: (*a*) ovary undeveloped or small; (*b*) ovary developing; (*c*) ovary well developed.

A total of 327 females were in berry, so that this represents a fourth phase in the reproductive cycle. In order to determine whether these berried females had resting or active gonads, 245 of them were dissected and their condition recorded under the same categories as before.

The results are summarized in Tables III and V and text-figures 6 and 7. The upper part of text-figure 6 shows the percentages of berried females, while the lower part gives the percentages of dissected females not in berry with gonads in one of the three different developmental stages.

Table III

The activity of the reproductive organs of female crabs at Sand Vlei during the period February 1947 to February 1948.

Date	*Females not in berry*				*Females in berry*	*Total number of crabs examined*
	Undeveloped ovaries	*Developing ovaries*	*Well-developed ovaries*	*Number of females larger than 14 mm. dissected*	*Percentage of females in berry*	
	%	%	%		%	
12·2. '47	71	28	1	93	1	136
11·3	96	4	0	112	0	152
25·3	100	0	0	47	0	67
15·4	100	0	0	37	0	40
6·5	68	30	1	47	0	50
27·5	3	26	71	35	52	67
6·6	11	56	33	9	33	27
19·20.6	44	22	33	9	64	25
18·7	17	0	83	6	85	39
30·7	0	33	66	12	78	54
12·8	13	25	63	8	79	39
26·8	8	25	67	12	76	51
23·9	33	33	33	3	94	54
13·10	10	20	70	10	55	22
13·11	25	33	42	12	20	25
25·11	54	31	15	52	30	77
16·12	64	29	7	41	10	49
9·1. '48	93	6	1	90	4	243
23·1	96	4	0	82	0	97

Table III and text-figure 6 show that there is a definite periodicity in the reproductive cycle of the female. The breeding-season is in the winter and the spring. During summer the ovaries are in a resting stage, but by May development starts to take place.

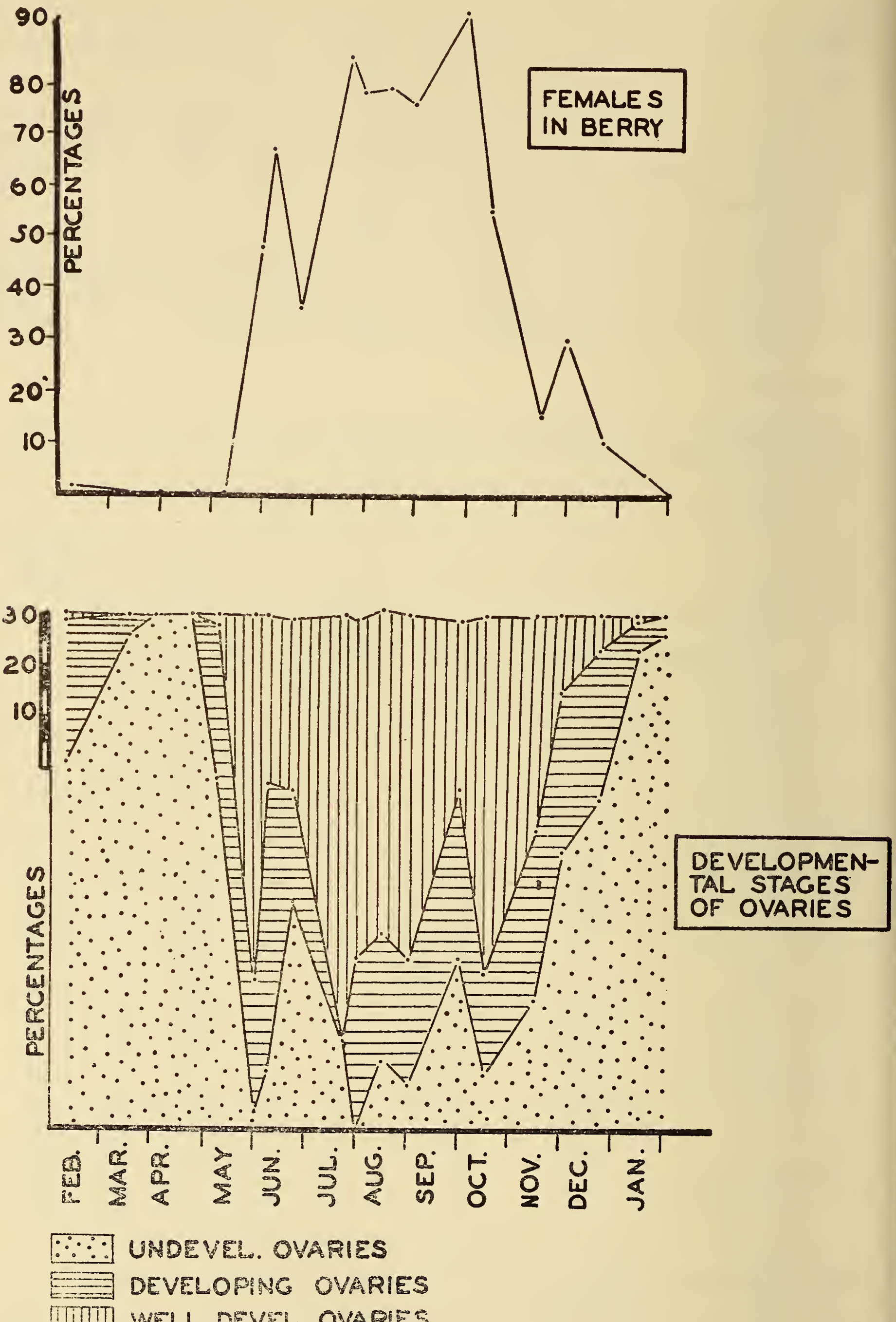

Fig. 6

The development of the gonads in females. The upper half gives the percentages of females in berry, while the lower half represents the percentages of dissected, not in berry, females with gonads in different developmental stages.

While the investigation was carried out plankton obtained in plankton netting in the Sand Vlei Estuary was also examined for the presence of larval stages. The results are given in Table IV.

Table IV

The occurrence of *Hymenosoma* zoeae in Sand Vlei Estuary.

Date	*June*	*July*	*August*	*September*	*October*	*November*	*December*
Quantity	some	some–many	some	many	many	few–some	few

As could be expected the presence of zoeae coincided with the months of the year that females were in berry.

As the breeding-season falls mainly in the winter, it coincides with the months of heavy rain and consequently Sand Vlei fills up with rain water. This eventually causes a strong current which flows into the sea so that large numbers of zoea larvae are lost to the estuary. As will be mentioned later the outflowing water will have a salinity too low for the zoeae to remain alive.

Table V

Analysis of samples of mature females from other localities.

	Total number of females	*Not in berry*	*In berry*
Lambert's Bay October 1946	226 = 100%	84 = 37% of these: 18% with undeveloped ovaries. 35% with developing ovaries. 48% with well-developed ovaries.	142 = 63%
Lambert's Bay December 1946	246 = 100%	192 = 78% of 117: 72% with undeveloped ovaries. 15% with developing ovaries. 14% with well-developed ovaries.	54 = 22%
Hermanus September 1947	160 = 100%	142 = 88% of 137: 2% with undeveloped ovaries. 37% with developing ovaries. 61% with well-developed ovaries.	18* = 11%
Berg River Mouth September 1949	94 = 100%	36 = 38% of 24: 54% with well-developed ovaries.	58 = 62%

* An additional 74 (46%) had still traces of hatched eggs.

Although there is a possibility that the tide sometimes may carry zoeae larvae into the estuary, those swept out will outnumber those swept in. The maintenance of the *Hymenosoma* population in the estuary must be in great part due to the limited number of zoeae which hatch when the mouth of the estuary is blocked by a sandbank, or when the mouth is still open while very little water flows out and the tide enters at high water. The possibility of crabs invading the estuary from False Bay cannot be completely ruled out.

As has been mentioned previously in addition to the crab material which was collected at Sand Vlei some was collected from other localities. *Hymenosoma* was extremely common in a small blind lagoon at Lambert's Bay, and in October and December 1946 material was collected and examined. In September 1947 material was collected from the large Hermanus lagoon and in September 1949 crabs were collected and examined from the Berg River Mouth.

The results are given in Table V. (See previous page.)

Many crabs were also kept in the laboratory. The salinity of the water in which these were kept varied from 2·7‰ to 30·9‰. This variation is not abnormal because under natural conditions the species occurs in places where large variations in salinity do take place. The temperature varied between 13° C. and 15° C. In seventy-one cases these crabs extruded egg-batches. In Table VI these have been tabulated according to the months in which they occurred.

Table VI

Egg-batches extruded by 34 crabs kept in the laboratory.

Month	*Number of egg-batches*	*Percentage of total number of egg-batches*	*Month*	*Number of egg-batches*	*Percentage of total number of egg-batches*
January	2	2·8	July	11	15·5
February	4	5·6	August	15	21·3
March	1	1·4	September	7	9·9
April	1	1·4	October	13	18·3
May	1	1·4	November	8	11·3
June	4	5·6	December	4	5·6

The information given in Table V indicates that the breeding-season for *Hymenosoma* females from Lambert's Bay, Hermanus, and the Berg River Mouth is similar to that from the Sand Vlei Estuary crabs. Table VI shows that under the stated laboratory conditions, egg-laying could take place in any month of the year, but mainly occurred from July to December. This also agrees with what was found at the Sand Vlei Estuary (see text-figure 6).

The Relationship between the Gonad Activity of the Two Sexes

If text-figures 5 and 6 are compared, it is clear that the short resting-period of the gonads of the males (from October to December) coincides with the last half of the breeding-period of the females. This may be expected, because copulation during the egg-carrying period must be down to a minimum. A similar state of affairs was found to exist in *Cyclograpsus punctatus* (Broekhuysen, 1941).

Number of Egg-batches extruded by each Female during a Single Breeding-Season

In order to ascertain whether one female produces more than one batch of eggs in a breeding-season, berried females were dissected and the state of the gonads recorded. If only one egg-batch was produced, the gonads of berried females could be expected to be in a resting stage; if, however, more than one batch of eggs was extruded, the gonads could be expected to be in various stages of development.

A total of 245 females in berry were dissected and the results are tabulated in Table VII which is graphically expressed in text-figure 7.

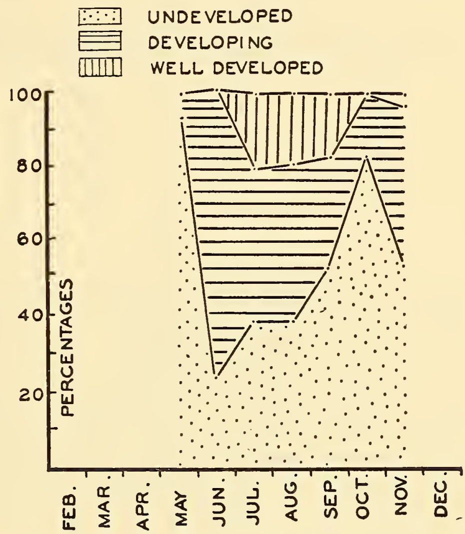

Fig. 7
Developmental stages of the gonads in females in berry.

Table VII

State of development of ovaries of berried females.

Date	*% females with undeveloped ovaries*	*% females with developing ovaries*	*% females with well-developed ovaries*	*Total number of crabs*
May	94	6	0	16
June	24	77	0	13
July	39	41	20	54
August	39	42	19	62
September	53	31	16	51
October	83	17	0	12
November	54	43	3	37

Table VII and fig. 7 show that in May most of the berried females had undeveloped or resting gonads. During the rest of the breeding-season (June to September) the ovaries were in various stages of development while the crabs were carrying developing embryos. This is strong evidence that more than one batch of eggs is produced per breeding-season. As shown below (Table VIII) these results were confirmed by observations on crabs kept in the laboratory.

Table VIII

The interval between the hatching of one batch of eggs and the laying of the next in between consecutive moultings in laboratory cultures.

Interval in days	*Number of cases*	*Interval in days*	*Number of cases*	*Interval in days*	*Number of cases*
9	2	17	3	36	1
10	1	18	2	39	1
11	2	19	1	42	1
12	2	21	2	43	2
14	2	32	2	48	1
15	2	33	2		
				Average interval 23 days	

From Table X the average incubation time of eggs kept under the stated laboratory conditions appears to be 43 days. The average interval between batches was 23 days (see Table VIII). The total time from the attachment of one egg-batch until the attachment of the next during the breeding-season was therefore about 66 days. The breeding-season during the period of the investigation lasted from May until October covering approximately 150 days. Although information obtained on crabs kept in the laboratory under controlled conditions may differ to some extent from what is the case for crabs under natural conditions, the possibility of two to three batches of eggs in one breeding-season may be provisionally accepted.

The Development of the Eggs in the Egg-batches

In the eggs of the marine Brachyura the following ten developmental stages can be distinguished by external examination of the living eggs:

Stage I. No segmentation has occurred and no external cleavage can be detected.

Stage II. The first cleavages have taken place.

Stage III. A considerable number of cleavages have taken place.

Stage IV. The first indication of invagination has become visible.

Stage V. A distinct division between a yolk-free and a yolk-containing part can clearly be seen. This stage covers the whole period between the first indication of the forming of the germ-layers and the formation of the eye-pigment.

Stage VI. The first indication of the eye-pigment is externally visible.

Stage VII. The first indication of the chromatophores which will form pigment bands has become visible.

Stage VIII. The larvae are clearly pigmented, a fair amount of yolk remains, but is becoming reduced in quantity.

Stage IX. The yolk has nearly disappeared, the egg-shells are rupturing, and the larvae are emerging.

Stage X. Only dead eggs and empty egg-shells remain.

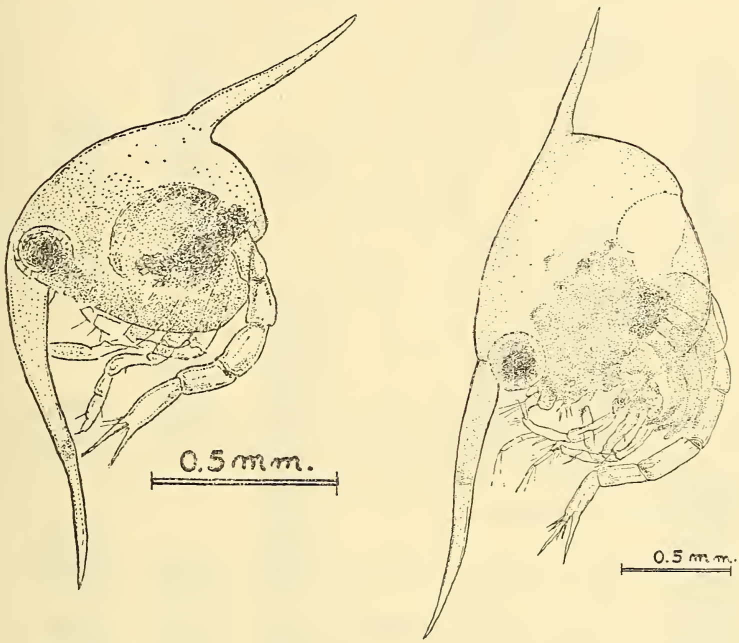

Fig. 8. *Hymenosoma orbiculare* Desm.
Left: first zoea stage; right: last zoea stage.

As in *Cyclograpsus punctatus* (Broekhuysen, 1941) it is the first zoea stage which escapes from the female abdomen (fig. 8, left).

During the period May 1947 to the first week of January 1948 a total of 323 egg-batches of berried females were examined and the stage of development of the embryos recorded. The results are given in Table IX. Individual variation in the development of one batch was slight and this was also found to be the case in other marine crabs (Broekhuysen, 1936, 1941). The duration of each stage was not the same and the laboratory experiments showed that the duration from stage I to beginning of stage IV was approximately the same as from stage IV to beginning of VII and stage VII to IX. In text-figure 9 stages I to III have been lumped together and the same has been done for IV to VII and VII to IX.

Table IX

The development of attached embryos during the 1947 breeding-season expressed in percentages.

Date	*Stage I*	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*I*		*Dead eggs*	*Total number of crabs*
	%	%	%	%	%	%	%	%	%	%	%	
27·5	3	9	25	19	31	6	0	6	0	0		32
6·6	0	18	12	18	41	6	0	6	0	0		17
20·6	0	0	11	11	11	11	0	0	0	56		9
18·7	0	0	16	3	25	3	28	25	0	0		32
30·7	0	2	14	12	14	0	10	45	0	0	2	42
12·8	13	3	13	3	10	3	3	50	0	0		30
26·8	5	5	21	5	24	5	5	24	0	3	3	38
23·9	4	4	14	4	16	6	0	49	2	0	2	51
13·10	17	17	25	8	8	0	8	8	0	0	8	12
13·11	22	11	56	11	0	0	0	0	0	0		9
25·11	0	3	6	0	8	6	6	69	0	3		36
16·12	0	20	20	20	40	0	0	0	0	0		5
9·1	0	0	0	0	0	0	10	90	0	0		10

Fig. 9 indicates that the majority of females produced two and perhaps three batches of eggs during the breeding-season of 1947 at Sand Vlei. This, therefore, confirms what has been said on page 324. Fig. 9 also indicates a considerable individual variation.

Incubation Times of Eggs kept under Laboratory Conditions

As has been mentioned previously crabs were kept in the laboratory while the field-work was in progress. The salinity of the water in which the crabs were kept was known at the beginning and the water-level was marked on the glass. At intervals distilled water was added to compensate for evaporation. At the end of the experiment (in some cases lasting over a year) the water in some of the dishes was titrated and the salinity determined. In this way a rough estimate of the salinity conditions during the experiment was obtained. As will be shown further on, the developing eggs of *Hymenosoma orbiculare* are rather euryhaline and the limited salinity changes of the water in the dishes will probably not be very important. The glass dishes containing the crabs were kept in a controlled temperature room. Most of the time the temperature was 13° C. but sometimes the temperature went down to 12° and up to 15° for a short time. The development of 43 batches of eggs extruded by crabs kept under these conditions was studied. The incubation time of all 43 batches was determined with an accuracy of two days. The results are given in Table X.

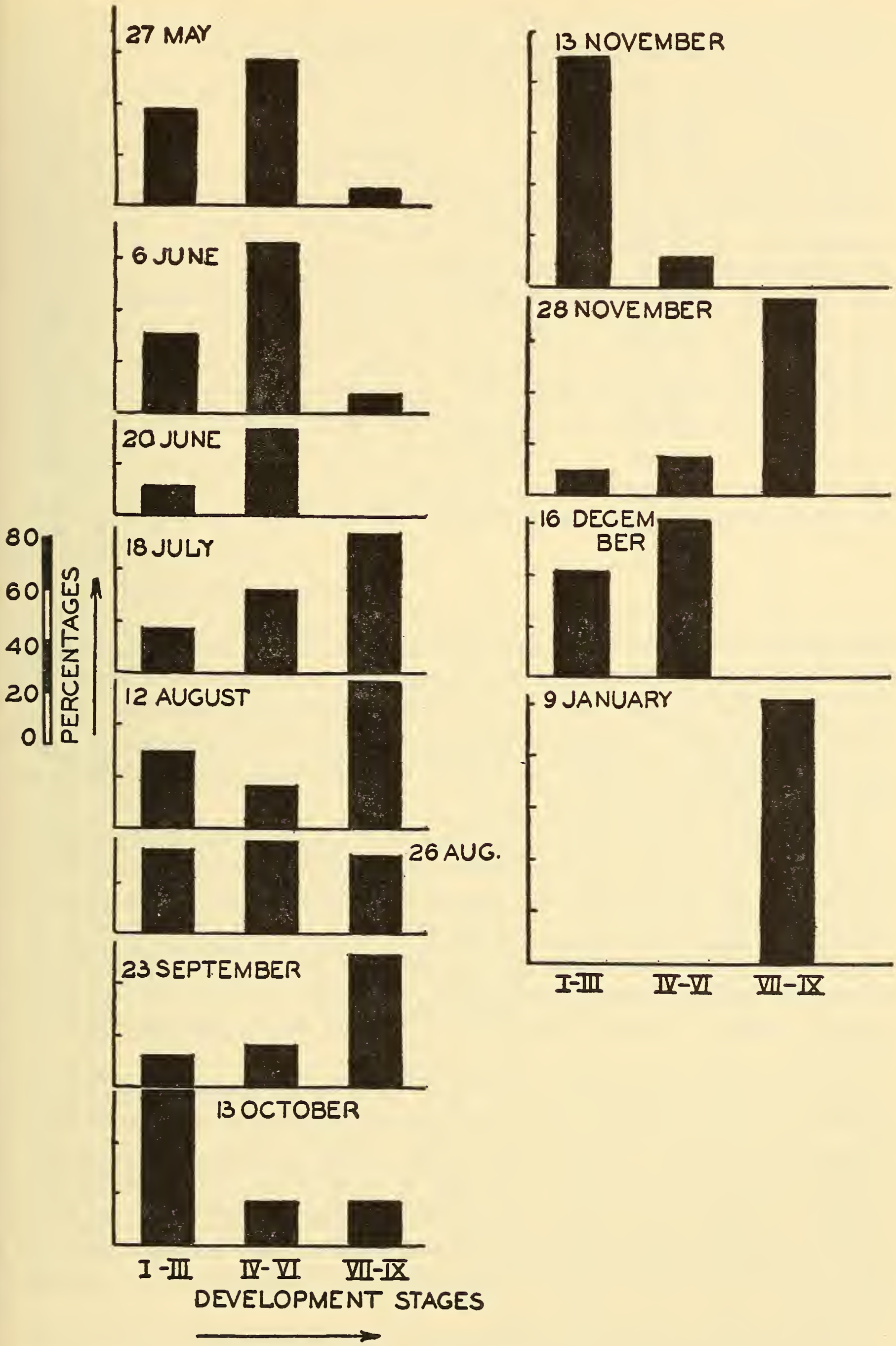

Fig. 9

The development of the attached embryos during the 1947 breeding-season expressed in percentages and three groups of development stages each of which takes about the same time. (The observations for 30 July are not graphed as they are practically the same as for 18 July.)

Table X

Incubation time of eggs under laboratory conditions.

Maximum temperature range	*Maximum salinity range*	*Incubation time in days*	*Average*
° C.	%		
12—13	15—29	49	49
12—14	14—29	43, 44, 47	45
	15—29	42, 43, 44, 44, 44, 44, 44, 45, 45, 47, 48, 48	45
	16—29	44	44
12—15	14—29	40	40
	15—29	43, 45	44
13—14	14—29	43	43
	15—29	39, 40, 41, 41, 42, 42, 42, 44, 44	42
	16—29	38, 39	39
13—15	14—19	41, 42	42
	15	41	41
	15—29	37, 38, 40, 41, 42, 43, 45	41
14	15—29	38	38
		Average of all observations	43

The figures in the above table show that 43 days was the average incubation time of the eggs of *H. orbiculare* at a temperature between 12° C. and 15° C. The figures also suggest that the more constant the temperature, the shorter the incubation time. A greater amount of variation of the temperature seems to increase the incubation time, as was also found to be the case for *Cyclograpsus punctatus* (Broekhuysen, 1941, p. 344).

In July 1947 a female with a carapace width of 18·7 mm., kept in a glass dish without any sand or shell fragments, extruded eggs which got attached to the hairs of the pleopods in the normal way. The presence of a soft substratum, therefore, seems not to be essential for a normal attachment of the eggs in this species. In this respect *H. orbiculare* seems to be different from *C. punctatus* and *C. maenas* (Broekhuysen, 1936, 1941) in both of which the extruded eggs did not get attached if sand and shell fragments were not supplied.

In laboratory cultures there were twelve cases of two batches of eggs being produced which developed normally although copulation had taken place only once, i.e. before the first batch of eggs. In two cases, three batches were produced after one copulation; the eggs of the first two batches developing normally while those of the third batch developed abnormally and never produced zoeae. There were four cases where three batches were extruded after one initial copulation and the eggs of all three batches developed normally into zoeae.

This shows that a female *H. orbiculare* can produce as many as three normal batches of eggs in succession although fertilized only by one initial copulation.

In some cases, however, the eggs of the third batch were not properly fertilized. The fact that one copulation suffices for the fertilization of more than one batch of eggs has also been found to hold good in other Brachyura (Gosse, 1852; Williamson, 1900; Churchill, 1917-18; Duncker, 1934; Broekhuysen, 1936, 1941).

In all the cases where small immature female crabs were put into the glass dishes and reared apart from males, the eggs developed only into an irregular cleavage stage and then died. In one instance four egg-batches were produced by such a female during a period of thirteen months. In this case none of the eggs developed further than into an irregular cleavage stage. In some cases females which had just moulted when caught were put into a glass dish. After some weeks these females moulted again, but as no male was in the dish, refertilization could not take place. Nevertheless the egg-batches produced later contained fertilized eggs, showing that the moulting process had not affected the spermatozoa stored in the female.

These cases also show that copulation is not essential for extrusion of eggs. The time between copulation and egg-extrusion varies considerably as can be seen from Table XI.

Table XI

The interval between moulting and the next egg-extrusion in the crabs kept in the laboratory.

Copulation took place after the moult				*No copulation took place*		
Date of moulting	*Date of copulation*	*Date of egg-laying*	*Interval in days*	*Date of moulting*	*Date of egg-laying*	*Interval*
14·3	17·3	31·5	77	25·3	3·6	59
30·4	30·4	about 24·6	54	1·4	6·8	126
22·5	22·5	5·7	43	6·4	1·7	85
25·5	25·5	7·8	73	13·4	6·7	83
19·6	21·6	29·7	39	27·4	19·6	52
21·6	21·6	27·8	66	27·4	10·8	104
3·8	?	7·10	64	28·4	25·7	87
3·8	?	22·10	79	6·5	about 2·7	57
11·8	11·8	8·10	57	12·5	10·8	89
11·8	11·8	26·11	106	15·5	4·7	49
22·8	22·8	about 15·11	84	15·5	18·7	63
9·11	11·11	28·1	78	19·5	18·8	90
9·11	11·11	12·2	94	26·5	31·7	65
15·11	17·11	5·2	81	26·5	23·9	118
1·12	1·12	9·2	69	4·6	4·8	60
	Average		71	10·6	10·8	60
				13·6	20·8	67
				17·6	7·11	142
				4·7	11·9	68
					Average	80

As shown later, copulation coincides with moulting of the female. If the two parts of Table XI are compared it will be seen that there is a difference of nine days between the average intervals, and copulation therefore seems to have a slight stimulating effect as regards egg-extrusion.

During the laboratory experiments several observations of the method whereby females with hatching eggs aided the zoea larvae to escape from underneath the abdomen were made. On such occasions females stood on their pereiopods and bent their abdomens backwards. The zoeae then poured from beneath the abdomen into the surrounding water.

Copulation

In *Hymenosoma orbiculare* copulation takes place between a hard male and a soft, newly moulted female. In this respect this species behaves in the same way as *C. maenas* and many other crabs. Copulation is preceded by an embrace of the female by the male, some time before she actually moults. The male holds the female underneath him with his pereiopods, but the female is in the normal position (i.e. dorsal side up). Actual copulation was observed several times in the laboratory. The following notes were taken on one of the occasions:

11·11. '47 Female recently moulted, leathery. Add male from dish 12. After a few seconds the male mounts the female. This male removed and substituted by male from dish 15. The latter, after a few seconds, approaches the female which is busy digging into the sand. Male is first on top of female, but then gets underneath the female. He then turns over on to his legs and in doing so keeps female underneath him and turns her over on to her back and copulation commences.

In the limited number of copulations observed, the process lasted more than half an hour and probably longer. After copulation had occurred, the female was kept embraced by the male for a considerable time, sometimes more than a day.

No actual experiments were carried out with a view to establishing the presence or absence of sex recognition. The general impression, however, was that sex recognition was poorly developed if present at all. The procedure in *H. orbiculare* seemed very similar to that suggested by Broekhuysen (1937) for *C. maenas*, i.e. the seasonal periodicity in copulation is only caused by the seasonal moulting act in sexually mature females, when the female due to its soft condition cannot evade or resist a male trying to copulate. These remarks, however, are tentative and more experimental work is necessary.

Growth

In order to obtain information on the rate of growth, the number of moults, the time required for hardening after moulting, the existence of sexual dimorphism and the average maximum age, all the crabs collected in Sand Vlei estuary were sexed and measured. The index of size used was the width of the carapace in millimetres. Crabs which were just about to moult, or had just moulted were noted. As has been mentioned a fairly large number of crabs were kept in captivity in some cases for periods of over a year. The growth of those which were caught while still small was recorded in order to supplement the data obtained in the field.

Moulting

As shown earlier, moulting not only marks a stage of growth, but in the present species it also controls the possibility of successful copulation. Moulting is thus essential to the animal but is also a dangerous period, for the crab is practically defenceless and open to attack by predators, including its own species. It has been noted that males copulate with soft, just moulted females and this must decrease the danger of soft females being attacked by males, considerably to the advantage of the females. In some cases females which moulted in the laboratory were killed by males in the same dish. If this was not an abnormal occurrence due to captivity, it means that the moulting female is not altogether immune to attacks by males. *Hymenosoma orbiculare* and also the other species of Brachyura where males copulate only with soft females seem to have some advantage over species in which copulation occurs between two hard crabs.

The process of moulting in *H. orbiculare* is identical to what takes place in other Brachyura and has been described for *Carcinus maenas* and *Cyclograpsus punctatus* by Broekhuysen (1936 and 1941). One interesting difference between the hardening of the new shell of *C. punctatus* and that of *H. orbiculare* was found. While *H. orbiculare* always remained submerged during the process, it was found that in *C. punctatus* it is essential that the crab should only be submerged part of the time for the hardening process to proceed normally.

The duration of the hardening process was observed in the laboratory. For 52 crabs between 8 and 22 mm. carapace-width at a temperature between 12 and 15° C., the average time was four days and the extremes two and nine days. Unfortunately the records do not permit one to determine the effect of temperature or the size of the crab on the duration of the hardening process.

The increase in size after moulting was recorded for 99 crabs kept in captivity under fairly constant temperature. These records include a certain number of observations on crabs kept in very low salinities and some which were kept in water with a salinity of over 35‰.

As the increase in size of crabs kept in abnormal salinities was roughly the same as the increase for crabs in normal salinities, the records were combined. Also, no significant difference was found between males and females. A summary of all the records gave the following results:

Size range	*Number of crabs*	*Percentage increase in carapace width*
5—8 mm.	15	22%
9—12 mm.	18	24%
13—16 mm.	48	15%
17—22 mm.	18	11%

Thus also in *H. orbiculare* the rate of increase decreases as the crab gets bigger and older.

Periodicity in Moulting

As females only copulate after moulting, it was thought possible that mature females would show a distinct periodicity in moulting, correlated with the breeding-season.

In Table XII percentages of moulting females and males, and females in berry have been combined. Only crabs larger than 14 mm. have been considered. The information is expressed graphically in fig. 10.

Table XII

Date	*% of moulted females*	*% of females in berry*	*Total number of females*	*% of moulted males*	*Total number of males*
February 1947	3	1	136	5	108
March	37	0	119	14	184
April	35	0	40	5	78
May	21	27	117	5	78
June	19	52	52	13	31
July	8	81	93	13	30
August	4	78	90	2	43
September	13	94	54	0	1
October	5	55	22	0	3
November	13	27	99	6	53
December	4	10	49	5	39
January 1948	4	2	338	4	159

From Table XII and fig. 10 it can be seen that mature females can and do moult during the whole of the year, but that there is a definite maximum in moulting activities during the months March, April and May. Fig. 10 also shows that this increase in moulting precedes the breeding-season. The observations available for the males seem to indicate that there is no clear maximum for the moulting in this sex.

In fig. 11 the comparable figures for crabs kept in the laboratory have been graphed. If the two figs. 10 and 11 are compared it will be noticed that they differ little for the females but quite distinctly for the males. The females kept in captivity also show a sudden increase in the number of moulting crabs in March, April and May, the same as was found in the crabs at Sand Vlei. For the males the number of observations of captive crabs is limited but they do show a clear maximum of moulting in March. This was not found in the crabs at Sand Vlei.

It should be stressed that fig. 11 is based on crabs kept under rather uniform conditions and may therefore be more accurate in a comparison of the behaviour of females to males. In any case it is interesting to note that in these laboratory crabs, the moulting activity of the males precedes the maximum moulting activity of the females, in other words the males have already moulted and become hard when the females moult and are ready for copulation. In the field where conditions are not uniform this adaptation apparently becomes less striking.

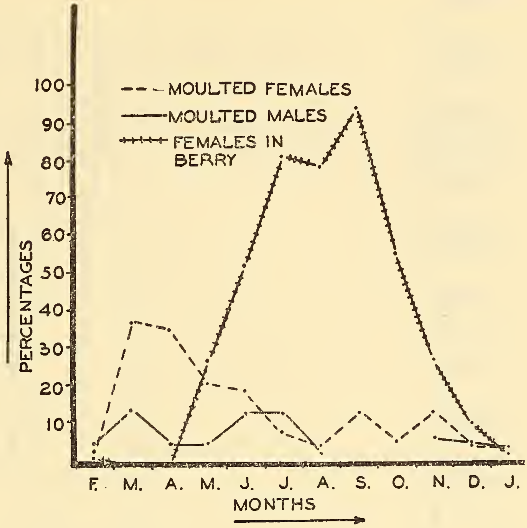

Fig. 10

The percentages of (*a*) moulted or moulting females, (*b*) moulted or moulting males and (*c*) females in berry, plotted against the months of the year. The crabs were collected at random at the mouth of Sand Vlei.

Sexual Dimorphism

In *Hymenosoma orbiculare* there is relatively little external difference between the two sexes except for the shape of the abdomen, and the development of the pleopods, which are adapted to carrying eggs in the female. The chelae, however, are somewhat bigger and broader in the case of the male (fig. 1).

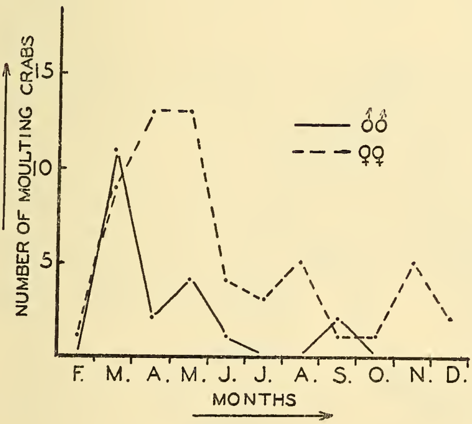

Fig. 11

The number of moultings taking place in the different months in crabs kept in captivity.

In order to determine whether there was a consistent difference in size between males and females of the Sand Vlei population, a total of 1,417 females, of which 316 were females in berry, and 856 males were measured. The results are given in Table XIII and graphed in fig. 12.

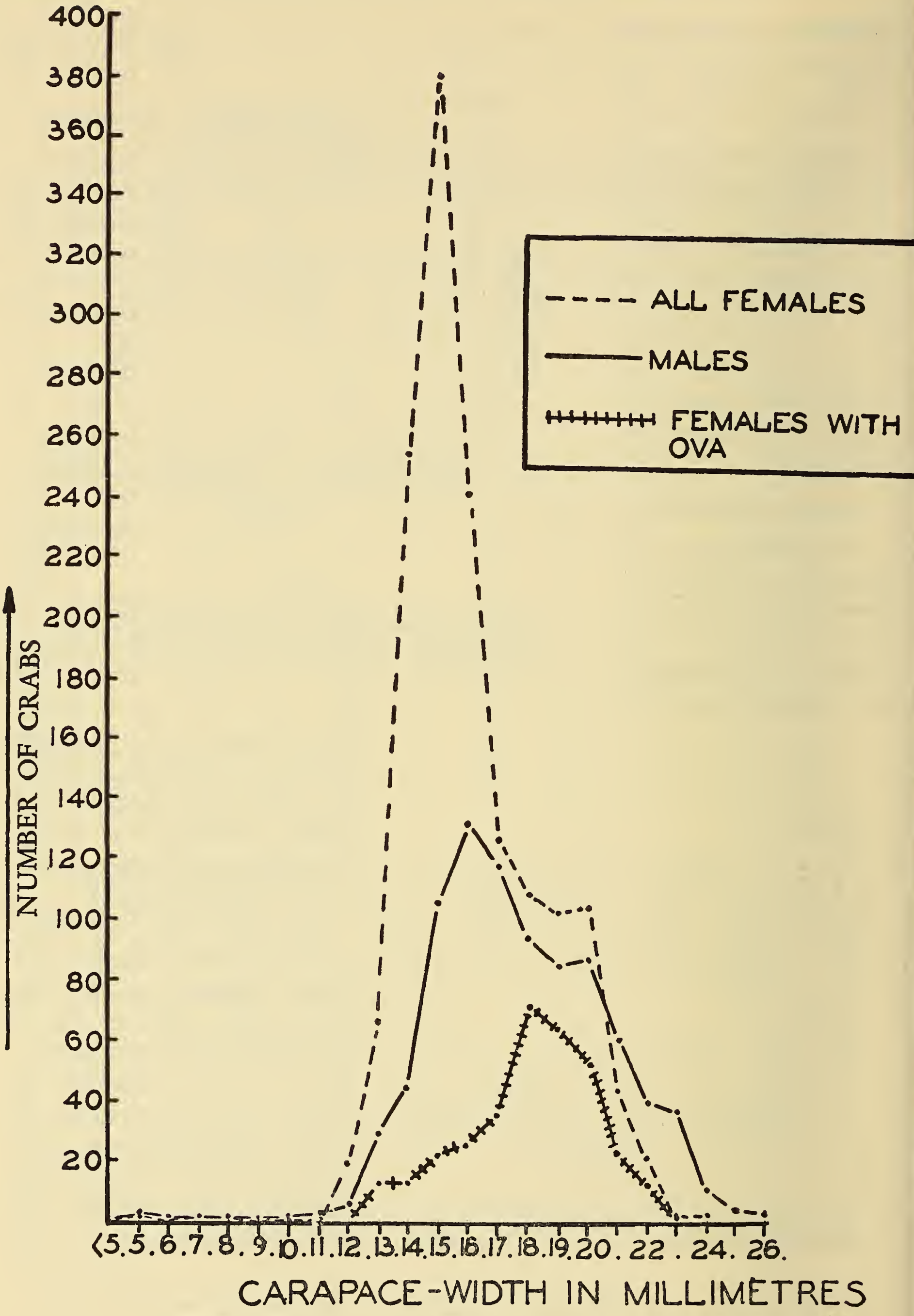

Fig. 12
The distribution of all the crabs measured over classes differing one millimetre. The size is expressed in carapace-width in mm. (females with ova means females in berry).

Table XIII

The carapace width in millimetres of crabs from Sand Vlei

Carapace width	*Females (those in berry included)*	*Females in berry only*	*Males*	*Mean carapace width for females*	*Mean carapace width for males*
5 mm.	–	–	1		
5	1	–	2		
6	–	–	1		
7	1	–	1		
8	1	–	1		
9	–	–	1		
10	1	–	1		
11	1	–	2		
12	19	–	5		
13	66	12	28		
14	254	12	44	16	18
15	381	21	105		
16	241	24	132		
17	126	35	118		
18	108	71	94		
19	101	64	84		
20	103	52	86		
21	43	22	60		
22	20	12	39		
23	2	1	36		
24	2	1	10		
25	–	–	3		
26	–	–	2		
Total	1,471	316	856		

The mean for females is 16 mm. and for males 18 mm. The difference is very small and was tested statistically. The *t*-test of significance showed that at the 1 per cent level of significance the estimated *t* was 2·819 and the 5 per cent level 2·074. The calculated value for *t* was 0·136. There was therefore no significant difference in size between the two sexes in the population of *H. orbiculare* at Sand Vlei at the time of the investigation.

The shape of the curves in fig. 12 may suggest the presence of two year-classes in both females and males.

The Rate of Growth

Since crabs can only increase in size when they moult the rate of growth is dependent on the increase at a moult and the frequency of the moults.

As has been mentioned before the experiments in the laboratory did not reveal any significant difference between males and females in the increase in size after a moult. The increase after moulting is mentioned on page 331. As regards the number of moults, or rather the duration of the interval between two successive moults, it is difficult, if not impossible, to obtain information on crabs living under natural conditions. The only information available, therefore, comes from crabs reared in the laboratory where conditions were not quite natural. This may or may not have affected the duration of the intervals between successive moults.

In Table XIV the available information has been tabulated. The females not in berry and those in berry as well as the sexes have been kept separate. The crabs have been divided into five size-classes.

Table XIV

Interval between successive moults in days, in crabs reared in the laboratory. (Extremes are given in brackets.)

	Females				Males	
	Not in berry		*In berry*			
Size in mm.	*Average duration*	*Number of cases*	*Average duration*	*Number of cases*	*Average duration*	*Number of cases*
5	40(18–58)	5			30(18–40)	5
5–8	33(25–45)	11			35(22–57)	4
9–12	52(30–90)	12			37(38–96)	5
13–16	89(59–139)	11	219(216–221)	2	32(81–214)	4
17–22	128(42–183)	5	174(109–221)	11	66(51–79)	4

This table reveals some interesting points:

(*a*) From the table it appears that the interval between successive moults, even in crabs of less than 5 mm., was considerable. For the smallest sizes this may be partly due to the young crabs taking some time to settle down to laboratory conditions after their capture.

(*b*) The interval between two successive moults even for crabs of the same size-class varied a lot.

(*c*) The table also shows that the intervals in the case of females in berry were considerably longer than those for females not in berry and males. The number of observations on males, however, may be too small to enable any positive conclusions, but they suggest that where the female growth can be affected adversely by breeding, this may not be the case for the males. This point will be mentioned again later.

(*d*) The interval gets longer as the crab gets older and therefore bigger and in this respect *H. orbiculare* behaves in the same way as other Brachyura.

In order to determine the development of the crabs at Sand Vlei, size/frequency graphs were plotted for each month of the year and for both sexes. These are given in fig. 13. While every attempt was made to obtain random samples, there is no doubt that a high proportion of the smallest size groups, particularly those under 7 mm., evaded capture. To this extent the samples and the graphs constructed from them are biased.

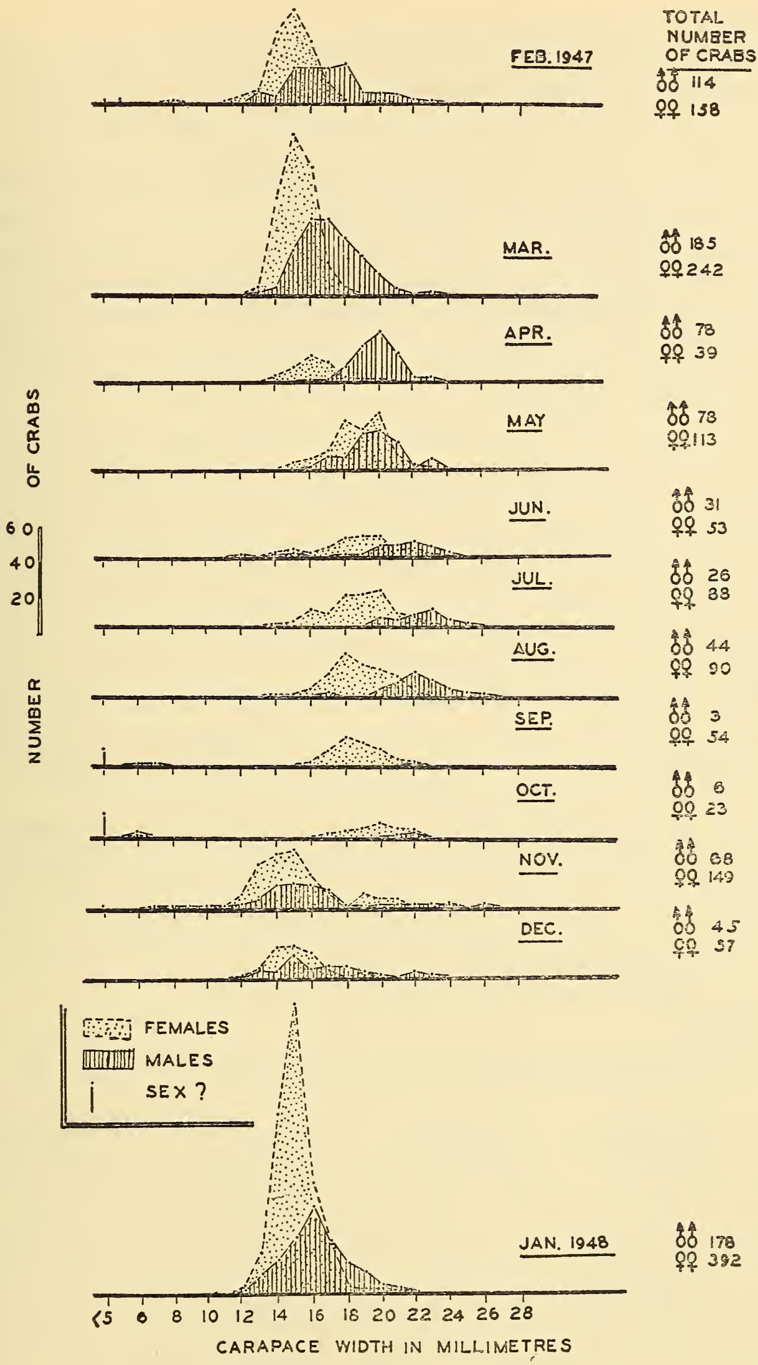

Fig. 13

Size/frequency of males and females for the different months. The crabs were all collected at the Sand Vlei mouth.

Even so the following important points are shown:

(*a*) In 1947 a considerable number of very small *H. orbiculare* made their appearance in the catches in September. These were the new generation of the year. In addition there were a considerable number of female crabs of 16 to 22 mm. carapace-width which were probably over 1 year old. Hardly any males were caught. In October the position had changed very little. In November a distinct group of female and male crabs of 12 to 18 mm. had appeared. It is unlikely that these consisted of crabs of the same season as they appeared too big for that. It is impossible to decide where these crabs came from, although the possibility of an invasion into the estuary from the shallow sea along the shore of False Bay cannot be ruled out. A certain number of crabs hatched in 1946 were still present, but by December most of these seemed to have vanished.

(*b*) If we examine fig. 13 we shall see that in November and December the curves for the males and the females more or less coincided. In January, February and March the males gained more and more so that by April there was a considerable difference in size between the males and the females, the former being the largest. In May, however, this difference suddenly disappeared due to a sudden increase in the size of the females. It should be remembered that March, April and May are months in which the females showed an increase in their moulting activity (see figs. 10 and 11), prior to the beginning of the breeding-season. During June, July and August the males again gradually gained on the females. This was the time when most females had egg-batches and therefore were not in a condition to moult. This did not affect the males (see Table XIV) which apparently continued to increase in size.

(*c*) In all months except April, there appeared to be more females than males and in September nearly all the males from the older generation had disappeared.

During the course of the investigation a number of very small *Hymenosoma* crabs were collected and reared in captivity. Some of the results of this part of the investigation have been combined in Table XV.

Table XV

Some small *Hymenosoma* crabs reared in captivity at 13° to 15° C.

Sex	*Increase in size in millimetres*	*Number of moults*	*Time in days**	*Salinity in parts per thousand*
♂	5 — 8	2	55	35
♂	4 to 5 — 13·5	5	230	35 — 36
♂	4 to 5 — 16	5	329	36 — 36
♀	4 to 5 — 13	4	169	31 — 35
♀	6·8 — 14·6	4	230	5 — 14
♀	4 to 5 — 13	4	252	5 — 10

* The number of days covers the period from the date of moult at which the smallest size mentioned was reached until the moult at which largest size mentioned was reached.

The above table indicates that crabs of about 14 mm. are more than 8 months old. It should be remembered, however, that these crabs were kept under unnatural conditions and fig. 13 seems to indicate that the crabs grow faster under natural conditions.

The size at which the crabs of the Sand Vlei population became adult

In males it was not easy to decide macroscopically when the crab had become mature. In females, however, the change in shape of the abdomen is an obvious indication of maturity. Moreover the development of the ovaries can usually be seen without the aid of a microscope. Extrusion of eggs is the surest sign of maturity having been reached. During the investigation the smallest females with 'adult'-shaped abdomen and the largest females with 'juvenile'-shaped abdomen were recorded and it soon became evident that a lot of variation occurred. Some females with a carapace-width as small as 12·2 mm. had 'adult' abdomens, while others as large as 17 mm. still had somewhat 'juvenile' abdomens. The smallest female carrying a batch of eggs was 12·6 mm. in the Sand Vlei population. Dissections showed that in one instance a female as small as 12·2 mm. had well-developed ovaries, indicating that she was mature. Dissections also revealed that some males of 12·3 mm. and 12·5 mm. had well-developed genital tubes, indicating that they were mature. In one instance a female of 15·5 mm. was collected that had a rather immature abdomen but dissection revealed well-developed ovaries. The shape of the abdomen, therefore, is not always decisive.

As will be seen later different environments may affect the minimum size at which maturity is reached.

Although the above data shows that *H. orbiculare* females from Sand Vlei could become mature at 12-13 mm., they were usually mature at 13-14 mm. carapace-width. This is confirmed in fig. 12 in which among others the size/frequency of berried females has been plotted.

Sex-Ratio

When all the sexable crab samples from Sand Vlei were added together it was found that 1,471 or 63·2 per cent were females and 856 or 36·8 per cent were males. It is interesting to note from fig. 13 that this predominance of females over males was specially marked in the January population. From then on the difference between males and females decreased gradually until in April the situation was such that there were more males than females. From April onwards the females again became predominant. No satisfactory explanation can be given for the large predominance of females over males. It is very unlikely that the males were overlooked during collecting. The increased predominance of females after May may be partly due to the fact, noticed during collecting of samples, that the females usually do not expose themselves so readily as the males and that, therefore, the chances of being swept away to the sea by the current are greater for the males.

Discussion

Although the fact that *H. orbiculare* is often found in estuaries indicates that the species is euryhaline, there seems to be a certain minimum salinity tolerance, as these crabs do not occur in waters with a constant very low salinity. In order to estimate this minimum salinity limit, crabs were kept in water of a low salinity and under controlled temperature conditions. These experiments showed that within a temperature range of 12°–15° C., a salinity of 5 per thousand interferes with the normal development of the eggs. Eggs extruded under these conditions did not develop beyond the first cleavage stages. However, when females carrying embryos in an advanced stage of development were kept under the same conditions, the embryos did hatch sometimes but the resulting zoea larvae died immediately. A salinity of 0·2–1·4 per thousand and a temperature of 12°–14° C. had the same effect on development.

Although salinities of 1–5 per thousand at a temperature of 12°–15° C. seriously affect the early development of this species if the crabs are exposed to these conditions long enough, it apparently has little or no effect if the crabs are only exposed to it for a short time. This is shown by the figures in Table I. From this table it can be seen that during part of June, July and August 1947 the salinity at the mouth of Sand Vlei fell well below 4 per thousand but this apparently did not affect the development of the larval stages in the egg, although it may have affected hatching zoeae and eggs freshly extruded. As the salinity in estuarine sands changes slowly, even when the water above is almost fresh, the habit of the females to dig into the surface layer of the sandy substratum may have saved the eggs from any adverse influence due to too low a salinity.

During the low-salinity experiments in the laboratory, several females extruded eggs. Low salinities, therefore, apparently do not prevent females from extruding eggs. Nothing definite can be said regarding the effect of prolonged exposure to high salinities, but there are strong indications that although the species may survive and even develop under these conditions, it has some effect.

Barnard (1950) in his Monograph on the South African Decapoda mentions a variety of *H. orbiculare* from deeper water in False Bay, which at first sight seems to be specifically distinct from the normal *orbiculare*. Although Barnard stresses the difference he does not consider it necessarily another species.

During the course of this investigation the present author had an opportunity of examining fairly large numbers of these deep-water *Hymenosoma* from False Bay. In addition to the extensive granulation, mentioned by Barnard, there was a striking difference in the size when compared with *H. orbiculare* from the mouth of Sand Vlei. In Table XVI the sizes of these deep-water crabs are compared with those of the Sand Vlei population.

Table XVI

Comparison of crabs dredged below 12 fathoms in False Bay with those from Sand Vlei estuary:

	False Bay (dredged)	*Sand Vlei*
Females		
Maximum carapace-width	10 mm.	24 mm.
Average carapace-width	7·9 mm.	18 mm.
Smallest ♀ with mature abdomen	6–7 mm.	13–14 mm.
Smallest berried female	6 mm.	12·6 mm.
Males		
Maximum carapace-width	12 mm.	26 mm.
Average carapace-width	7·6 mm.	18 mm.

The total number of deep-water crabs available was 96 ♀♀ and 85 ♂♂. The differences in size between the two populations are very striking. If the deep-water crab is the same species as *H. orbiculare* which populates the mouth of Sand Vlei, the difference must have been caused by external conditions. The factors which may be concerned are:

(*a*) constant high salinity in the case of the False Bay crabs, and a lower average salinity, but varying tremendously, in the case of the Sand Vlei population;

(*b*) considerable depth in the case of the False Bay crabs, and relatively shallow water in the case of the Sand Vlei crabs;

(*c*) a less variable temperature in the case of the False Bay crabs.

Without more detailed field-work and experiments, it is not possible to be certain which of these factors is or are the more important. There is some evidence, however, that salinity may be important. In 1948 during an investigation of the ecology of St. Lucia Estuary on the Zululand coast (Day, Millard and Broekhuysen, 1954) it was found that salinities in this estuary were very high (34–53 per thousand). Specimens of *H. orbiculare* were collected and measured, and it was found that females were becoming mature at 5 and 6 mm. carapace-width and one female of 4 mm. had a 'mature' abdomen. Several berried females were only 5 and 6 mm. These crabs were therefore comparable, at least as far as size, with those from False Bay. Although few measurements are available the *Hymenosoma* crabs inhabiting Langebaan Lagoon also seem to be of small size. The smallest mature female measured was 10 mm., while a female of 7 mm. carrying an egg-batch was collected in Saldanha Bay into which Langebaan Lagoon opens. The salinity in this lagoon is near the salinity of normal sea-water and therefore fairly high.

It seems, therefore, that high salinity is at least one factor which decreases the size of the mature crabs. It also increases the size of the chelae in the males and causes excessive granulation. There are also indications that there is a difference in breeding habits between the deep-water *Hymenosoma* from False Bay and those from Sand Vlei.

When the *Hymenosoma* results are compared with those for *Cyclograpsus punctatus* (Broekhuysen, 1941) it is evident that there is a great deal of similarity between the two species. Both are winter-breeders. In *C. punctatus* breeding covers the period May to November and in *H. orbiculare* the period is from June to November. In both cases the females produce several egg-batches in the one breeding-season. Whereas *C. punctatus* has a second, minor breeding-season in the summer this is not evident in *H. orbiculare*. In both species the gonads of the male show a periodicity in their activity which is adapted to the rhythm in the females. There is also a great similarity as regards the incubation period of the eggs of the two species. The incubation time of the eggs of *C. punctatus*, at a constant temperature of 16·5° C., is little over a month, while at a temperature of 12°–15° C. it took the eggs of *H. orbiculare* 38 to 48 days to develop and hatch.

In *Cyclograpsus* copulation takes place between two hard crabs while in *Hymenosoma* it only takes place between a hard male and a freshly moulted female. In *C. punctatus* no seasonal difference between the moulting periods of the two sexes was observed, while in *Hymenosoma orbiculare* such a difference did seem to occur. This is probably related to the fact that in the latter copulation only takes place when the female has recently moulted. In neither species is there a significant difference in size between the two sexes. In *C. punctatus* from the shore of False Bay the majority attained an age of two to three years. The present investigation indicates that the majority of *H. orbiculare* die in their second year. In both species there were more females than males, although this appeared to be much more pronounced in the case of *Hymenosoma*.

Summary

(1) *Hymenosoma orbiculare* is a crab which occurs in the shallow waters of estuaries as well as in deeper water along the shore of South Africa and Portuguese East Africa. Most of the material on which this paper is based was collected in the False Bay area between February 1947 and February 1948.

(2) The population, showed a definite periodicity in the activity of the gonads and the breeding-season appeared to be the winter months.

(3) *Hymenosoma* females extruded two or three egg-batches during the breeding-season.

(4) The development of the eggs was followed in the field and in the laboratory.

(5) Females will only allow males to copulate after the female has moulted and is still soft.

(6) Although moulting may occur at any time of the year, the females showed a sudden increase in moulting a few months before egg-extrusion.

Under laboratory conditions males also showed a periodicity, which seemed to be adjusted to that of the females. Under natural conditions this was not so evident.

(7) Evidence is given that during the breeding-season males increase more rapidly in size than the females. This may be due to the fact that the majority of females are carrying eggs and therefore do not moult during that period.

(8) The percentage increase in size of the crab after each moult shows a gradual decrease as the crab grows larger.

(9) The size at which the female crabs became mature was established for the Sand Vlei population for the period of the investigation. In crabs from other localities it was found that the size varied according to environment.

(10) There was evidence that the majority of crabs, in the population studied, reached an age of somewhat over one year, after which a heavy mortality occurred.

(11) There are the usual Brachyuran sexual differences between the male and the female *Hymenosoma orbiculare*; but there is no significant difference between the sizes of the two sexes.

(12) Of all the crabs collected and sexed 63·2 per cent were females and 36·8 per cent males.

(13) The influences of low and high salinities are discussed and the life history of *H. orbiculare* is compared with that of *C. punctatus*.

Acknowledgement

I have pleasure in thanking Professor J. H. Day for his valuable criticism.

REFERENCES

Barnard, K. H., 'Descriptive Catalogue of South African Decapoda Crustacea (Crabs and Shrimps).' *Ann. S. Afr. Mus.*, XXXVIII, 1-864, 1950.

Broekhuysen, G. J., 'On Development, Growth and Distribution of *Carcinides maenas* (L.).' *Arch. Neerl. Zool.*, II, 257-399, 1936.

——, 'Some notes on Sex Recognition in *Carcinides maenas* (L.).' *Arch. Neerl. Zool.*, III, 156-64, 1937.

——, 'The Life-History of *Cyclograpsus punctatus*, M. Edwards: Breeding and Growth.' *Trans. Roy. Soc. S. Af.*, XXVIII, 4, 331-6, 1941.

Churchill, E. P., 'Life History of the Blue Crab'. *Bull. U.S. Bur. Fisher.*, 36, 1917-18.

Day, J. H., Millard, N. A., Broekhuysen, G. J. B., 'The Ecology of South African Estuaries, Part IV, The St. Lucia System.' *Trans. Roy. Soc. S. Af.*, XXXIV, 1, 129-56, 1954.

Duncker, H., 'Gefangenschaftsbeobachtungen an *Sesarma cinerea* Milne Edwards.' *Zool. Jahrb. Syst.*, 66, 285-90, 1934.

Gosse, P. H., 'On the Sloughing of the Spider-Crab (*Maia squinado*).' *Ann. Nat. Hist.*, X, 210-12, 1852.

Williamson, H. C., 'II. Contribution to the Life-History of the Edible Crab (*Cancer pagurus* Linn.), 18th.' *Rep. Fisher. Board Scotl.*, 3, Sci. Invest., 77-143, 1900.